THE CAMBRIAN FAUNAS OF NORTH-EASTERN AUSTRALIA.

PART 4: EARLY CAMBRIAN ECHINODERMS SIMILAR TO THE LARVAL STAGES OF RECENT FORMS.

By F. W. WHITEHOUSE, PH.D., D.SC.

(DEPARTMENT OF GEOLOGY, THE UNIVERSITY OF QUEENSLAND).

(Plates I–IV.)

Summary: In the lowest zone of the Middle Cambrian of Queensland two species of unattached echinoderms occur in vast numbers. One of these, bilaterally symmetrical, corresponds morphologically to the dipleurula stage in the larval history of the phylum. The other agrees with the radially symmetrical form that, in ontogeny, usually succeeds that stage. Stereom structures are more simple than is usual for the echinoderms; but a change in skeletal structures by the adoption of fibrous spherulitic growth provides an explanation for the metamorphosis in echinoderm ontogeny and the attainment of pentameral form. Some observations are offered upon the inter-relationships of the major groups of the phylum.

From the Lower Cambrian to the Ozarkian echinoderms are richly present in the sequence of Western Queensland. Very often the ossicles are packed so closely, with relatively little of the calcareous cement, that they form echinodermal limestones as fully organic as the typical crinoidal limestones of later periods. Such limestones often are of great thickness as well as of wide extent. Usually, however, as with later limestones, the plates are so closely adpressed that the surface features of individuals or the form of the whole skeleton is not to be determined. Yet from quite a number of horizons, from late Lower Cambrian to Ozarkian, united ossicles of normal pelmatozoans have been obtained. These will be described at some later date. Meanwhile this record is given of two members that are not pelmatozoans but belong to quite a new group. They occur in vast numbers and in considerable perfection; and they have features of unusual interest for morphological and phylogenetic studies in the phylum.

THE MATERIAL AND ITS AGE.

The specimens were collected in 1939 by Mr. Edgar Riek* and myself on Thorntonia station in the far north-west of Queensland (lat. 19° 30′S.: long. 138° 55′E.). During this field period a wonderfully rich assemblage of Cambrian fossils (sponges, brachiopods, molluscs, trilobites and echinoderms) was obtained from measured horizons throughout the whole range of the Middle Cambrian and part of the Lower Cambrian. When described they will amplify considerably the stratal and faunal notes given in previous parts of this publication. A summary has been published elsewhere (Whitehouse 1940, p. 45) of the stratal succession, with a record of a few of the trilobite horizons.

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* I take this opportunity of expressing my thanks to Mr. Riek for his very great assistance both during the field work and in later activities.

Essentially in North-Western Queensland the sequence is of limestone. Occasionally chert beds (some of them original, siliceous sediments, others being later replacements of the limestones) occur as prominent bands in the section. Around Thorntonia the sediments belong to the upper part of the Lower Cambrian and the lower part of the Middle Cambrian. The pertinent portion of the sequence for the present purpose is shown graphically in figure 1.

The Middle Cambrian limestones in this region are over 800 feet in thickness. Through the first 150 feet the trilobite genus *Xystridura* occurs, often in very great abundance. Immediately below are beds with *Redlichia* but with very little else—only echinoderm ossicles, *Orthotheca* and *Helcionella*. Actually the two trilobite genera overlap for two feet in their ranges. In the *Xystridura* beds a number of new trilobite genera appear, particularly towards the top of the stage, all of them Middle Cambrian types—for instance *Pagetia* and *Lyriaspis*. Other rich Middle Cambrian faunas (with *Nepea* and *Amphoton*) appear in the immediately succeeding beds. Such relationships, together with the mesonacid affinities of *Redlichia* and some as yet unpublished work upon the agnostids, suggest that the incoming of *Xystridura* may best be regarded as the beginning of the Middle Cambrian. *Redlichia*, on this reading, dies out at the beginning of that division.*

Both echinoderms now to be described have been found only in the early part of the *Xystridura* zone. They have been collected on hills adjoining the left bank of the Thornton River, one mile south of the present Thorntonia homestead. *Cymbionites* appears first in the basal beds of the zone (about ten feet above the river flats) and lasts until the initial two feet of the second limestone (bed E of figure 1). Thus, on present evidence, it ranges through forty feet of strata. At its final appearance it occurs in colossal numbers. The limestone is closely packed with complete specimens of the echinoderm, weathering out beautifully upon the surface. A flat-lying, slabby limestone with specimens crowded as richly as in pl. I, fig. 1, and as well preserved, may be traced continuously around the contour of these hills. Following it is like walking over thickly strewn, embedded marbles. The fecundity of this species is astonishing.

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* In previous parts of this publication, when no sequence of the beds had been traced in the field (collections having been made at sporadic localities), a zonal nomenclature was used based solely upon the palaeontological evidence. Now, however, a continuous section has been traced through the whole of the Middle Cambrian limestones and collections carefully have been made. The succession of trilobites and other forms thus has been established by direct observation so that some revision of the zonal scale is desirable. The trilobite stages of previous nomenclature are of unequal value. Some of them need to be modified. For instance the association of *Nepea* and *Amphoton* occurs at intervals through a very large part of the Middle Cambrian and seems to have mainly a facies significance. There are, however, few changes to be made. For the present, until this evidence can be presented in detail, Middle Cambrian beds vertically as far as the horizon with *Dinesus* may be placed in the one zone—a *Xystridura* zone.

Twenty-four feet above this rich band occurs the bed, five feet thick, with *Peridionites*. This is packed almost as tightly with specimens as the other (pl. I, fig. 2) and they, too, weather out in relief. *Peridionites*, so far as is known, is restricted to this bed. Between the two rich horizons are other echinodermal limestones greatly crowded with ossicles that, however, do not stand out with naturally etched surfaces. Thus what echinodermal types occur in them is unknown. They may be largely of normal pelmatozoans; for definite, conjoined, pelmatozoan ossicles occur throughout this range, from the beds with *Redlichia* to the *Peridionites* band.
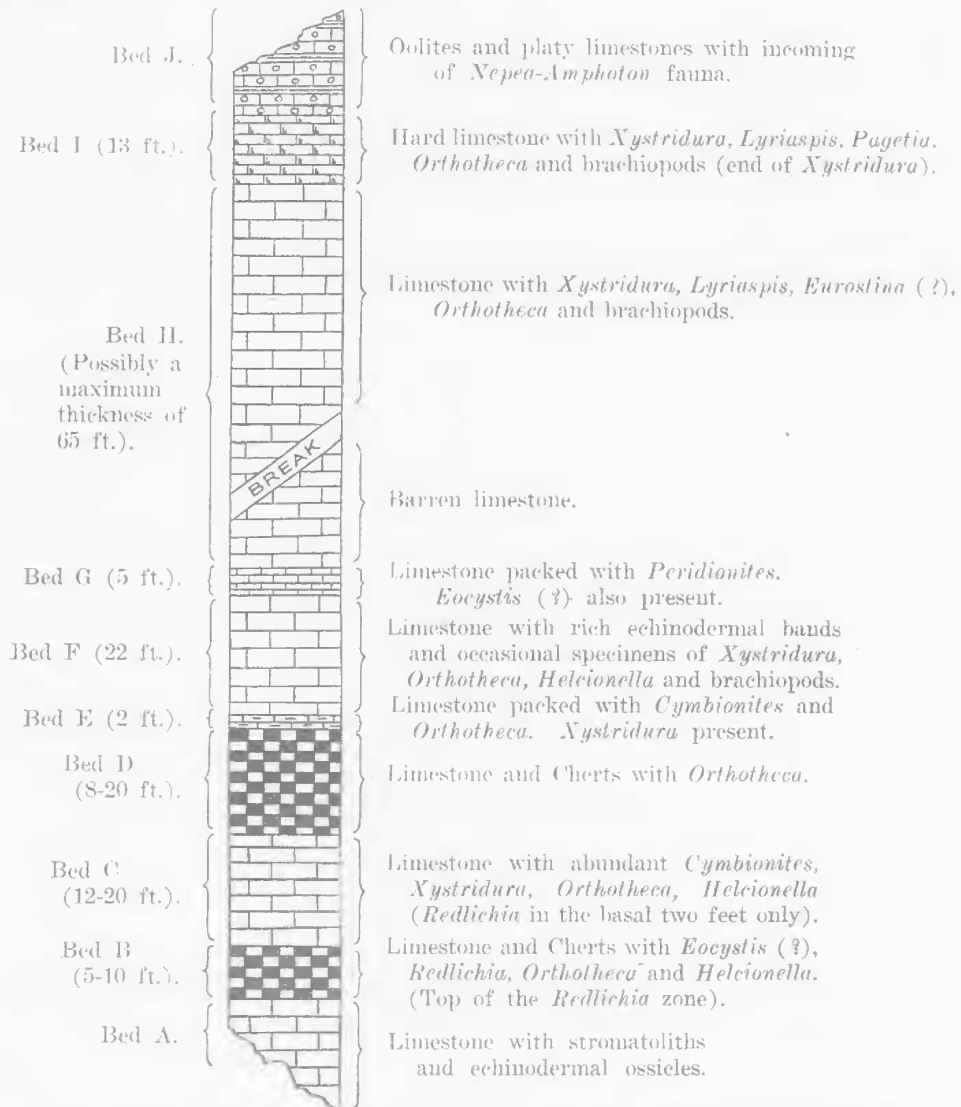

Bed J.
Oolites and platy limestones with incoming of *Nepea-Amphoton* fauna.

Bed I (13 ft.).
Hard limestone with *Xystridura, Lyriaspis, Pagetia, Orthotheca* and brachiopods (end of *Xystridura*).

Bed H. (Possibly a maximum thickness of 65 ft.).
Limestone with *Xystridura, Lyriaspis, Eurostina* (?), *Orthotheca* and brachiopods.

BREAK

Barren limestone.

Bed G (5 ft.).
Limestone packed with *Peridionites*. *Eocystis* (?) also present.

Bed F (22 ft.).
Limestone with rich echinodermal bands and occasional specimens of *Xystridura, Orthotheca, Helcionella* and brachiopods.

Bed E (2 ft.).
Limestone packed with *Cymbionites* and *Orthotheca*. *Xystridura* present.

Bed D (8-20 ft.).
Limestone and Cherts with *Orthotheca*.

Bed C (12-20 ft.).
Limestone with abundant *Cymbionites, Xystridura, Orthotheca, Helcionella* (*Redlichia* in the basal two feet only).

Bed B (5-10 ft.).
Limestone and Cherts with *Eocystis* (?), *Redlichia, Orthotheca* and *Helcionella*. (Top of the *Redlichia* zone).

Bed A.
Limestone with stromatoliths and echinodermal ossicles.

Fig. 1.—The succession of beds in the *Xystridura* zone (basal Middle Cambrian) on Thorntonia Station, showing the echinoderm horizons.

These are the only collections that yet have been made from the beds so that all collected specimens, including types, are lodged in the Geology Department of the University of Queensland. Examples of both forms will, however, be placed in the Queensland Museum, and slabs with *Cymbionites* are being sent to the Australian Museum, the British Museum, the Sedgwick Museum and the American Museum of Natural History.

STATE OF PRESERVATION.

The plates of the theca in each species are preserved as crystalline calcite, each plate being one optically continuous crystal. There has been, however, some late silicification, so that both outer and inner surfaces, to a varying depth, have been silicified. This is most marked in *Cymbionites craticula,* the outer skin of which commonly has the familiar multiple rosettes of beekite. In complete specimens some silicification of the articulating surfaces has gone on, so that specimens such as that of pl. II, fig. 11 are quite common, in which outer and inner surfaces of the theca and the articulating surfaces of the plates have been converted to silica and stand out, while the non-silicified remainder has dissolved away.

The lower limestone (bed A in figure 1), of the *Redlichia* zone, often has numerous grains of coarse, quartz sand, suggesting some current action. In the basal limestone of the *Xystridura* zone (bed C) the trilobite fragments, occurring in enormous numbers, are broken into pieces, the shattered parts being tightly packed in several bands. *Cymbionites,* in this bed, occurs more frequently as isolated plates than as complete specimens (pl. I, fig. 3). In the later limestone band the specimens are complete (pl. I, fig. 1), and isolated plates are very rare. In the *Peridionites* band, where separate plates are prolific (pl. I, fig. 2), complete thecae are found only occasionally. Both echinoderms have very firm sutures. Turbulent conditions, breaking shells and skeletons, seem thus to have alternated with quiet phases during the deposition of these limestones.

DESCRIPTION OF THE SPECIES.

PHYLUM ECHINODERMATA KLEIN, 1734.

Sub-Phylum HAPLOZOA nov.*

In this new division are placed such early, unattached echinoderms that have a skeleton composed of few plates, forming a theca about an unrestricted calyx. Bilaterally and radially symmetrical members are known; and since they have differing micro-structures, and since bilaterally and radially

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* ἁπλόος simple, ζῶον living creature.

symmetrical stages are separate and distinct in the early ontogeny of living echinoderms these two groups, the Cyamoidea and the Cycloidea that must have each only a few members, are for convenience regarded as separate classes.

Class **CYAMOIDEA** nov.

The bilaterally symmetrical members of the group, with a small, pouch-like or bean-shaped theca (κύαμος, a bean) composed of five plates. The stereom is not formed of prismatic fibres.

Family PERIDIONITIDAE nov.
Genus **PERIDIONITES** nov.*

Genotype: *Peridionites navicula* sp. nov.

Diagnosis: Unattached echinoderms with a skeleton composed of a reniform theca that is bilaterally symmetrical about two planes, is closed aborally, and consists of five plates—an apical plate (dorso-centrale), two end plates and two medio-lateral plates, the latter being bounded by the converging end plates.

PERIDIONITES NAVICULA sp. nov.
(Pl. I, fig. 2; Pl. II, figs. 1–9.)

Description: The individuals are small, pouch-like structures, laterally compressed and sub-semi-circular in outline. They are bilaterally symmetrical about both the sagittal and transverse planes. There are five, massive, calcareous plates in the theca, enclosing a calyx that has the maximum width and length of the theca. The outer surfaces of the plates are unornamented and the articulating surfaces are smooth. The stereom is not fibrous but has radiating and rather irregular pores.

Fig. 2.—Lateral and ventral diagrams of *Peridionites navicula* (× 5).

The two end plates, at the limits of the sagittal axis, are similar and are the largest plates of the theca. They are rhomboidal in lateral view, subtriangular in transverse section, and have slightly curved outer edges. On each the ventral face has three shallow depressions, separated one from another by two radial grooves. The largest of these (the Axial Depression) is subovate and occupies most of the surface, continuing to the outer edge of the theca. Towards the centre of the theca this is flanked by two similar, smaller, subtriangular pans (the Lateral Depressions). The inner surface of the plate is faceted about a median, channelled ridge, the two facets being the articulating surfaces for the medio-lateral plates. The dorsal or aboral surface, where the apical plate adjoins, is smooth and subtriangular.

The medio-lateral plates are subtriangular, with the free edges prominently arched. Such a plate has a cuneate section adjacent to the theca calyx,
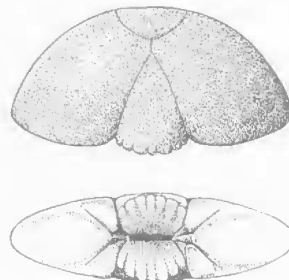
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* πηρίδιον, a small pouch.

where the inner face is radially grooved. Between the medio-lateral plates and the inter-facet ridges of the end plates is the relatively deep, central portion of the calyx, the Central Fossa.

The apical plate (or dorso-centrale) is a small, wedge-shaped structure with smooth, curved surfaces. No trace has been found upon it of any place of attachment for the theca.

There is no evidence of any tegmen.

The calyx thus is divisible longitudinally into five sections symmetrically arranged—the anterior axial depression, the paired antero-lateral depressions, the central fossa, the paired postero-lateral depressions and the posterior axial depression. The symmetry is such that, from the skeleton alone, no distinction can be made between anterior and posterior structures, the two ends being precisely similar. The central fossa is moderately excavated for some depth and then, towards its base where the medio-lateral plates come closely together, becomes slot-like by the development of a narrow, aboral, tongue-shaped cavity, the Central Cleft. The grooves on the inner surfaces of the medio-lateral plates and the bounding grooves of the lateral depressions together form a system of radiating channels around the main portion of the central fossa.

Variation: Thirty-six complete or almost complete thecae have been examined and many hundred isolated plates. There is a considerable variation in the lateral outline of the theca, as is shown by the figured specimens. Usually the vertical axis is shorter, occasionally considerably shorter, than the sagittal, but some forms in this are equidimensional. The majority of the specimens are markedly compressed in the transverse plane, with a sub-fastigate outer edge. But there are a few forms more obese and with a broadly arched edge. Nevertheless there is no marked division into two or more definite types, so that advisedly all are retained in the one, variable species.

In the more compressed forms the central fossa is an elongate structure, but in the more obese forms it is broadly ovate in oral view. The number of grooves on the inner surfaces of the medio-lateral plates is not fixed, so that there is a slight variation in the number of radiating grooves around the central fossa.

Dimensions: For comparison the length of the sagittal axis of each suitable, complete specimen is stated in millimetres with the transverse and vertical dimensions given, for each specimen, as a percentage of this. Such dimensions for six specimens are as follows:—

Catalogue Number.	Sagittal Axis.	Transverse Axis.	Vertical Axis.	Reference (if figures).
F. 5399	9·4	56	45	Pl. II, fig. 1
5400	9·4	78	42	Pl. II, fig. 2
5401	10·0	77	42	Pl. II, fig. 3
5402	8·8	85	40	Pl. II, fig. 4
5403	9·2	57	38	Pl. II, fig. 5
5404	11·0	55	33	Pl. II, fig. 7 (holotype)

Interpretation : From the foregoing observations the following conclusions may be drawn about the body of the species :

1. The body was segmented, five segments being recognisable.

2. About the transverse plane there was a perfect symmetry in the outward form of the segments, and there was an equally perfect symmetry of the body parts about the sagittal plane.

3. The soft parts were seated in eight regions corresponding to the eight depressions of the calyx, that in the central fossa being the most voluminous.

4. All openings that the species may have had (oral, anal and hydroporal) were on the one side (ventral) of the body. The other side (dorsal) was arched.

5. The radiating channels around the central fossa indicate a set of radiating structures, most probably muscular ligaments by which the body was attached in the calyx.

The bilateral symmetry of the calyx, and thereby of the form of the body, together with the arched dorsum and the ventral placing of essential openings, are reminiscent strongly of structures in the larval form (dipleurula stage) of present-day echinoderms. One difference only is noticeable—hydropores, if present, must have been ventral in position. The comparison may be taken much closer. Some other structures that are claimed as essential in the Dipleurula or ancestral form of the echinoderms (see, for example, Bather 1900, p. 4) are :

1. A pre-oral lobe.

2. A coelom divided into paired anterior and paired posterior portions.

3. An uncoiled intestine with possibly an enlargement to form a stomach.

The paired lateral depressions of *Peridionites* indicate the presence of anterior and posterior paired, soft structures of similar form, and suggest that they may have been the place of lodgment of the four, paired, coelomic sacs. Axially beyond these were equal, laterally unpaired structures, seated in the axial depressions. One of these corresponds in position with the pre-oral lobe. The other is a posterior lobe; and from the symmetry a post-anal lobe is suggested, thereby implying the presence of an anus. The most bulky portions of the body were centrally placed, and a stomach is indicated. Dorsal to this was a narrow, elevated portion of the body seated in the central cleft. In the echinoids, asteroids and ophiuroids the genitalia are borne in an aboral sinus, so that a similar function may be suggested, tentatively, for this aboral pouch. Suggestively, therefore, the structure of the body is interpreted as follows:

The animal, whose form would be of the type shown in figure 3, was segmented into five regions and provided with both mouth and anus as well as with an uncoiled intestine increasing medially to form a stomach. There were pre-oral and post-anal lobes of equal size, seated in the axial depressions. Paired coelomic sacs, two anterior and two posterior and all of equal size, were

present on the lateral depressions. The stomach was situated in the central fossa, this region of the body being attached to the inner, calical surface of the theca by a series of muscles. The hydrocoel, if present, would have been in the central fossa. But if it were present it must have been different from those of present day echinoderm larvae; for it would have been symmetrical (present forms are unsymmetrical or unpaired) and the hydropore would have
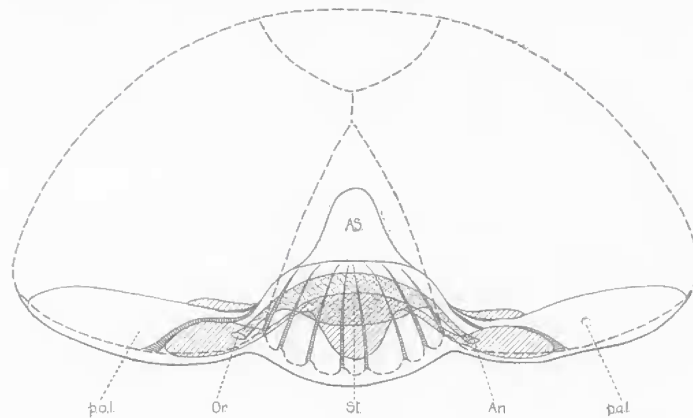

Fig. 3.—Interpretation of the soft structures of *Peridionites navicula*. Stippled area, the digestive tract. Lightly ruled area, the coelomic sacs. Heavily ruled areas, the muscles. *As.*, aboral (? genital) sinus; *An.*, anus; *Or.*, mouth; *p.o.l.*, pre-oral lobe; *p.a.l.*, post-anal lobe; *St.*, stomach. The presence of median coelomic sacs is questionable.

been on the ventral side. A symmetrical hydrocoel divided into two sacs is, of course, claimed usually as a feature of the theoretical Dipleurula. But the impossibility of there being a dorsal pore raises the question of whether in this form a water vascular system was present. Possibly there was, in the central fossa, a median pair of coelomic sacs that had not, at this stage, been modified to form a hydrocoel although, more likely perhaps, there may have been no median, coelomic sacs. Aborally was a pouch (the aboral sinus) containing the genitalia.

From such premises the Cyamoidea have claims to include the ancestral, dipleurural form of the phylum. It is doubtful whether *Peridionites* itself, a form of the littoral benthos with very thick plates, is a primitive member of the class. Somewhat simpler forms yet may be expected from the Lower Cambrian or even older rocks. Yet from the perfection of its segmentation it possibly is not far removed from the direct lineage of the Dipleurula.

Class **CYCLOIDEA** nov.

The radially symmetrical members of the group, with a small, cup-like theca (κύκλος, a circle), composed of five radially disposed plates with possibly an apical plate.

Family CYMBIONITIDAE nov.

Genus **CYMBIONITES** nov.*

Genotype: *Cymbionites craticula* sp. nov.

Diagnosis: Unattached echinoderms with a skeleton typically composed of five equal, thick, curved, wedge-like plates united laterally and apically to form a cup-shaped theca arranged about a fluted, crater-like calyx. A membranous theca probably was present.

CYMBIONITES CRATICULA sp. nov.

(Pl. I, figs. 1 and 3; pl. II, figs. 10–24; pl. III; pl. IV.)

Description: The skeleton typically is composed of five, similar, very massive, wedge-shaped plates, the stereom of which consists of uniform fibres arranged in spherulitic form. Each plate is convex externally, has flat, smooth, articulating surfaces and a flat or slightly convex calical surface. In combination the plates form a theca with a smooth, uniformly rounded, external surface varying from hemispherical to thimble-like and even barrel-like or saucer-like in form. The theca is rigid, with the plates strongly adherent in spite of the lack of any articulating furrows, and sutures are not visible except on weathered specimens. The calyx varies considerably in form due to the variation in the angle made by the calical surfaces of the plates with the horizontal plane. In some types it is shallow, almost saucer-shaped. In others it is deep and crateriform. According to the straightness or curvature of the calical slope the calyx may be regularly conical or bell-shaped. The surface of the calyx is fluted by fine,

Fig. 4.—The general form of *Cymbionites craticula* and one radial plate (× 3).

straight channels that vary considerably in number. The plates in any one specimen are not always equal in size. A transverse section beyond the region of the calyx frequently reveals the presence of a small, additional and central, pentagonal plate (fig. 6c), not shown on the surface, being completely enveloped by the five radial plates. Other small, adventitious radial plates are sometimes present, either extending across the thecal radius or else limited to the central region. The calical edge is scalloped and bears a faint circum-oral groove suggesting that a membranous integument was present forming a tegmen.
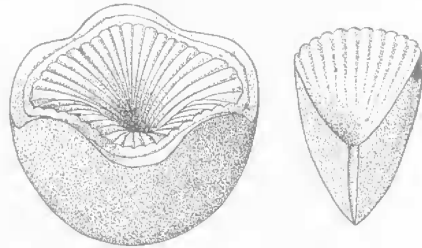
Variation: From the specific description, from the figures, from the measurements that are given, and from the arrangement of fibres described below, it will be seen that, in spite of the essential simplicity of the form, this is a very variable species. Several thousand specimens have been examined;

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* κυμβίον, a small cup.

but there seems no justification for regarding them as of more than one species. There is no uniformity of shape, although the hemispherical, capsular form is most frequent, and the number of plates is not always five, as is indicated in the following chapter. There seems to be variation also in the size attained by the adults. A diameter of approximately 12 mm. is so common that this may be regarded as the normal size of the fully grown form; but quite a number of specimens reach a diameter of 18 mm. There is such a host of still smaller specimens that considerable latitude in the size of the adults seems likely.

Dimensions: In this species the maximum transverse diameter is the standard chosen and is stated in millimetres. The length of the vertical axis and the depth of the calyx are stated as percentages of this. Such measurements for twelve specimens are as follows:

Catalogue Number.	Transverse Diameter.	Vertical Axis.	Depth of Calyx.	Reference (if figured).
F. 5409	14·3	97	39	Pl. II, fig. 12
5410	12·6	49	8	Pl. II, fig. 13
5411	11·5	104	57	Pl. II, fig. 14
5412	11·0	80	36	Pl. II, fig. 15
5413	11·5	104	56	Pl. II, fig. 16
5414	10·4	95	52	Pl. II, fig. 17
5415	8·3	127	..	Pl. II, fig. 18
5416	8·7	82	47	Pl. II, fig. 19
5417	8·6	76	35	Pl. II, fig. 20
5418	8·0	107	62	Pl. II, fig. 21
5419	8·0	114	80	Pl. II, fig. 22
5420	10·5	67	43	Pl. II, fig. 24

Interpretation: From such observations the following conclusions may be drawn about the soft parts:

1. The body was seated in a radially symmetrical calyx that was closed aborally.
2. Such symmetry that the body parts had was pentameral but some variation from the pentameral form occurred.
3. All essential openings of the body were ventral (oral) in position.
4. The calyx was fluted with grooves that possibly indicated the seating of muscles.

The great thickness of the plates and the close sutures render it impossible that there was an anal pore in the dorsal region. Thus either no anus was present, as in some present-day larval forms, or else (as in the crinoids) it had emerged on the oral side.

THE STRUCTURE OF THE STEREOM.

The fabric of the skeleton in *Peridionites navicula* is massive, non-fibrous calcite, each plate an optical unit with self-contained cleavage, and with the substance pierced by many, irregular, radially elongate and radially directed pores. Presumably the pores indicate that the plates were infiltrated by mesodermal tissue that was not sufficiently arranged in stromal form to develop spicular secretion. No trace has been seen in microsections of concentric arrangements that suggest growth lines.

In contrast the stereom of *Cymbionites craticula* is formed of packed, but intermittently impinging prismatic fibres (see pl. IV, figs. 3,4), between which is a meshwork of calcite in optical continuity with the fibres. The fibres of each plate are of uniform diameter (approximately 12 μ) and they unite as the one crystal of calcite having the characteristic cleavage pattern. But there are some significant departures, in the direction of decreased specialisation, from the stereom structures of living species. In such later forms an ossicle microscopically is a unit, the fibres being so arranged that in pattern each plate is a discrete entity. In *Cymbionites* the prisms of one plate have a definite relationship with those of adjoining plates; and there is a uniform, simple grouping for the theca as a whole (see pl. II, fig. 10 and text-fig. 5).
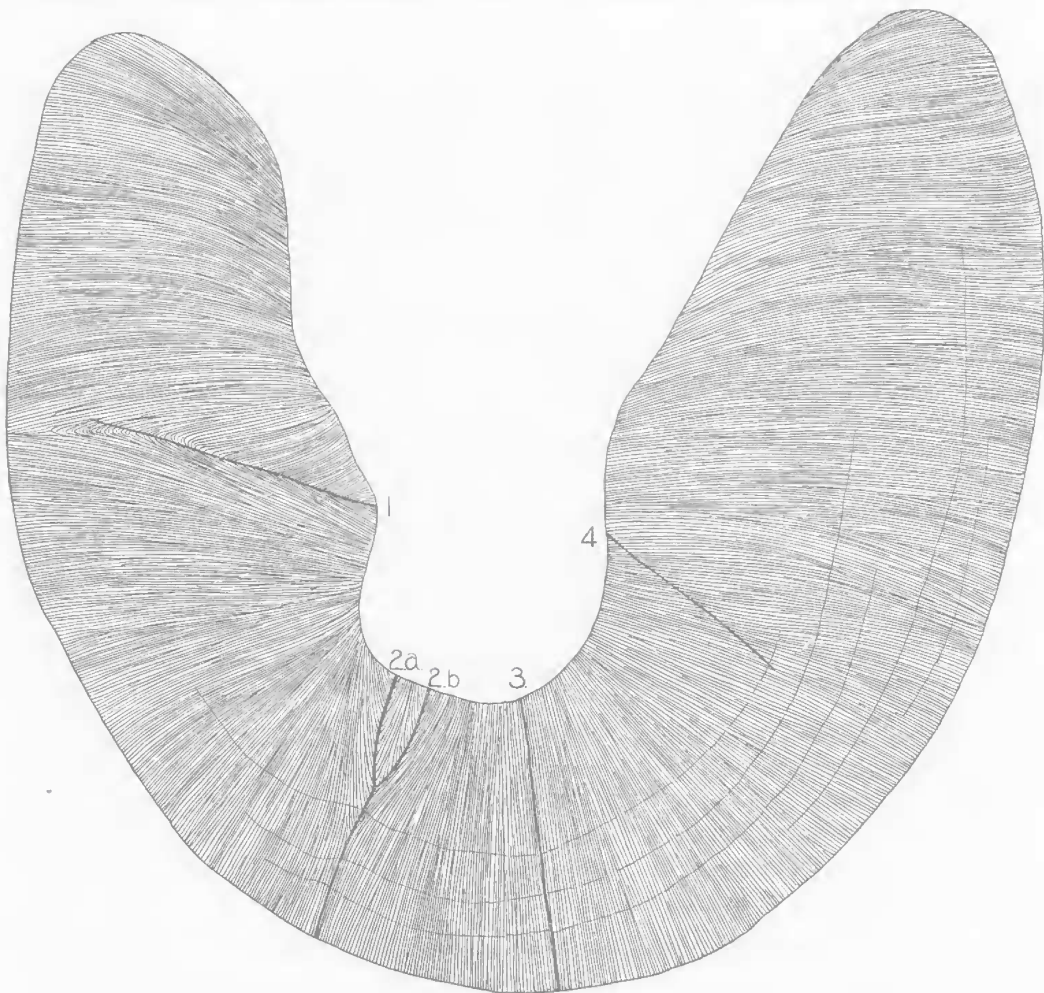

Fig. 5.—*Cymbionites craticula.* Semi-diagrammatic figure of plate II, fig. 10 (a vertical section), to show the unity of the fibrous arrangement throughout the whole skeleton, and the relationship of sutures to the fibres. Sutures nos. 2 and 3 are concordant; no. 1 is slightly discordant; and no. 4 is wholly discordant. The discordant sutures do not continue to the outer margin. Between the two branches of no. 2 is a subsidiary, internal plate, formed by a complete, minor tuft.

The fibres are arranged in two patterns—plumose, when they spread radially and arcuately from an axis; and tufted, when they arise at the calical margin and diverge as a uniformly spreading bundle (see plates III and IV). The fibres in a bundle slowly increase in number towards the limits of the tuft or plume by a process of branching or insertion of new fibres. Typically there is one plume or one tuft to a plate; and when the fibres, spreading outwards, reach the suture between an adjacent plate the individual prisms are matched symmetrically by the fibres of that adjoining ossicle (pl. IV, fig. 2). In tufted forms the fibres radially outwards become parallel to the sutures; but nearer the calyx, where they approach at slight angles, the individual structures are seen generally to be in apparent continuity, about this acute angle, from one plate to the next.

In all this there is a certain unity, or rather there is an alternative pattern according to the fibres being tufted or plumose. That is to say, there is one distinct bundle of prisms to each plate; and the bundle of one plate is a unit, visually separable from the adjacent bundle, even though some individual fibres seem symmetrically to cross the sutures. Actually, however, forms that keep strictly to this mode are rare. Among the more noticeable departures from type the following are significant:

1. Very occasionally (pl. III, fig. 3) the axis of a plume is the vertical axis of the theca; in which mode the theca may form one great bundle and apparently is not divided into plates by sutures.

2. Two or more tufts, or rarely two plumes, may occur within one plate (pl. III, fig. 2).

3. The radiating fibres of adjacent plates may meet symmetrically but the suture between may not strictly conform to this plane of symmetry (pl. II, fig. 10).

4. It may happen (pl. III, fig. 4) that a suture is aligned obliquely and discordantly across very straight prisms that continue their course unaffected by the suture. In the specimen illustrated one suture only is of this type. The other sutures of the theca are normal.

5. Well defined sutures may start at the inner wall, bounding a plume or tuft, but they disappear before reaching the outer wall, so that a plate does not separate (pl. IV, fig. 1).

From these vagaries it is obvious that there is generally a correspondence between the formation of sutures (and so of plates) and the natural division of the theca into unit bundles of fibres. But since the sutures do not always follow strictly the division planes between the bundles, and since also they are not always complete, they and the plating are evidently subsidiary in development to the arrangement of the fibres.

The tufted and the plumose forms denote two types of thecal growth. In the former the increase is outwards from the calyx; and the fibres are arranged normal to the growth lines—that is to the growing surface (see pl. II, fig. 10). Plumose forms presumably indicate that increase took place not only outwardly but also inwardly, in the direction of the calical wall. Where all

plates of the theca have plumose fibres the axes of the several plumes are at the same distance from the calical wall. Furthermore the axes of the plumes are relatively close to the calyx; so that increase in this direction was uniform but less than outwards growth (text-fig. 6D).

One curious circumstance is at present difficult to explain. In spite of the uniform pattern in any one theca the plates are individual crystals of calcite. Even in that remarkable type, No. 4 just mentioned, where the suture cuts obliquely across continuous fibres, a section under crossed nicols shows that on opposite sides of the suture the calcite extinguishes differently. The deduction from such evidence seems again to be that development of the sutures, and the welding of the fibres of each plate into the one crystal unit were subsidiary to the production of the fibrous form. And yet the specimen just illustrated is one of the largest thecae; and presumably in earlier stages of growth it had the usual crystal relationships. If so, as it increases in size, the individual fibres, continuous as units across the suture, divided at that plane in their crystal affinities—the one portion growing in optical continuity with its lateral neighbours, and the other, across the suture, having a corresponding relationship with its adjacent fibres. It is somewhat analogous though not of course homologous with the phenomenon of twinning in crystals.

A related feature that also as yet is unexplained is that occasionally circumscribed patches occur within one plate that optically are foreign to it but are in accord with the properties of an adjacent plate.

Realising what lack of uniformity there is in the grouping of the fibres it is not to be wondered at that the form of the theca varies to the degree that has been recorded in the description of the species.

Two far-reaching conclusions may be drawn from a study of the micro-structures. The first is that the fibres of a growing skeleton are aggregated precisely in the mode of spherulitic growth. That is to say, they follow the system of growth of a developing mass of inorganic, needle-like crystals of constant composition in a viscous medium. The second is that this growth is the primary cause of the symmetry of the skeleton, and that the symmetry of body parts is evolved in response.

The factors and forms of spherulitic growth have been analysed very clearly by Bryan (1941); and Bryan and Hill (1941) have shown, as a corollary, that in at least one group of relatively simple organisms with a fibrous crystalline skeleton, the hexacorals, skeletal growth is in accord with these principles. From Bryan's studies it is shown that the radiating, prismatic crystals of a spherulite grow in one of three modes—tufted, plumose or strictly radially—forming a distinct pattern that varies among spherulites but is constant for the one specimen. Bryan has pointed out, further, that a compound spherulite, growing about a spherical surface without interference from neighbouring structures, assumes naturally the form of a pentagonal dodecahedron superimposed upon a

spherical surface; and many of his specimens correspond, with some modification, to this ideal form. From this it follows that the majority of sections through such a structure will show a pentagonal arrangement of segments—as indeed is apparent from published figures (for example Bryan 1934, pl. 8; and 1941, pl. 3).

The typical pentagonal arrangement of tufts and plumes in the theca of *Cymbionites,* even though the form is subglobular and not spherical, are, by comparison, almost ideally grouped in spherulitic form. But in inorganic, spherulitic growth, although the pentagonal form is typical, specimens with fewer or more segments are common. Similar also are the skeletons of *Cymbionites.* There may be five tufts or plumes in a complete transverse section (the typical form), giving rise to five plates; there may be more than five bundles but still only five plates; there may be as many as seven fully
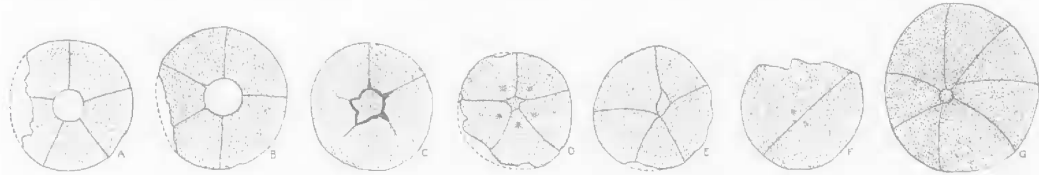

Fig. 6.—Drawings made from microslides across the theca of *Cymbionites craticula* to show variations in plating. A, a transverse section through the base of the calyx, with five subequal, tufted plates. B, similar to the preceding but with the plates unequal. C, a section beyond the calyx with a well-developed centrale but with only two sutures persisting to the outer margin. D, a plumose form with five subequal plates and a small centrale; the axes of the plumes, denoted by asterisks, are uniformly arranged around the main axis (microphotographs of this slide are shown as pl. IV, figs. 2, 3 and 4). E, a tufted form with a sixth plate. F, a vertical, tangential section through a plumose form. G, a transverse section, beyond the calyx, of the specimen shown in pl. II, fig. 23, showing seven unequal radials and a centrale. All sections except F are transverse sections and the magnification of each is slightly under two diameters.

developed radial plates in the cycle, each corresponding to a bundle (fig. 6G); the cycle may start with more than five plates but in outward growth be reduced to five by the crowding out of minor plates (pl. II, fig. 10); or, as a limiting condition in the other direction, only one bundle may be present in the theca and no subdivision into plates. Such a wide limit of variation, which is illustrated on the accompanying plates and text figures, is more in accord with ordinary, spherulitic growth than with a strictly biological control, which latter influence, if dominant, would determine the symmetry and the number of plates according to some organic constant.

And so the conclusion almost inexorably arises that the radial symmetry of the Cycloidea is due to spherulitic growth, determined by the condition that the skeleton is composed of uniform, acicular crystals growing in a relatively free medium (the mesoderm); and that the division of the theca into plates was occasioned by this mode of growth. As a corollary it appears that any corresponding pentamerism of body parts is not primary but has been induced

by the symmetry imposed by the spherulitic form. However, since *Peridionites* already had a longitudinal pentamerism of body parts this correspondence may have developed very quickly and naturally by a simple torsion of body structures.

In genesis, therefore, *Peridionites* and *Cymbionites* are diametrically opposed. In the former acicular fibres do not occur, and the skeleton conforms to the structures determined by the symmetry of the body. In *Cymbionites*, with fibrous growth, the spherulitic form develops, becomes the control, and the body is adaptive.

One factor may be important as a control. Both *Peridionites* and *Cymbionites* have unusually thick plates for an echinoderm. Were spherulitic growth to be initiated in a group with thin plates it is perhaps difficult to conceive that the process could control the growth. That in these forms, apparently, it did so may be related to the relatively great mass of the skeletal parts.

If the logical implications of spherulitic growth are taken to their limit one peculiar coincidence emerges, depending upon Bryan's demonstration that the ideal form of such a spherulite is a pentagonal dodecahedron. It is mentioned without emphasis as an interesting possibility that scarcely can be more than interesting while only the one genus of Cycloidea is known. A pentagonal dodecahedron has twelve sides; and about any axis through the mid point of a face this resolves itself into two polar faces and, between them, two cycles each of five faces. If spherulitic growth were the control in building the skeleton and the oral pole of the body became such an axis, the natural form of the skeleton would be of eleven plates—a centrale, a first cycle of five plates (the radials), and a second similiar cycle (terminals). The twelfth plate, by need of an oral, polar opening, would not appear.

Such a skeleton, modified in the dicyclic crinoids by the presence of a third cycle of plates, does happen to be the form assumed immediately after metamorphosis by all classes of living echinoderms that have an interlocking skeleton. Thus, since the features of spherulitic growth are so closely simulated or realised in *Cymbionites,* it may be that this form of the test also is a related feature. Cycloidea accordingly may include other genera with thinner plates, with a well developed centrale, and with a second cycle.

In the light of the finer, stereomic structures of *Cymbionites* two features of echinoderm morphology deserve investigation. There are, within the phylum, two contrasted but sporadically operating tendencies, one to increase the number of plates in any system, and the other to reduce the number. The former is exemplified by the remarkably variable plates around the dorso-centrale in *Uintacrinus,* so clearly described by Springer (1901), and by the more regular plates in the centre of the apical disc of Saleniidae. Sometimes the need for this increase is functional, as for instance with the anal plates of crinoids; but such an explanation seems inadequate for the two

examples quoted. Springer (1901, p. 35) suggested that something analogous to the variability of *Uintacrinus* might be expected at earlier periods (*Uintacrinus* is a Cretaceous crinoid). To casual appearances that prediction is realised with *Cymbionites,* in which the variation is due to the vagaries of spherulitic growth. It is a matter worthy of some attention whether, in such forms as *Salenia* and *Uintacrinus,* the multiplication of plates around the aboral pole is likewise due to modifications in the grouping of the fibres of the stereom.

In the reverse direction are such features as the formation of compound ambulacral plates in the diademoid echinoids, the syzygy of crinoids, and the remarkable reduction of the skeleton in *Tiarechinus* and its allies. Many of these economies seem to be effected in response to functional requirements; but how the mode of fusion operates (possibly it may be by new groupings of stereom units) does not seem to have been investigated.

Microscopic studies on these lines might even lead to some clarity in the vexed problem of the significance of monocyclic, dicyclic and pseudomonocyclic forms among the crinoids.

COMPARATIVE ONTOGENY.

After passing through preliminary blastula and gastrula stages the developing echinoderm, in all groups of the Eleutherozoa, attains a pelagic, bilaterally symmetrical form. There are individual differences in the arrangement of the ciliated bands and the arms that may arise to support them, but the general pattern is the same. This was established long ago by Müller (1853) who gave a series of names (Pluteus, Auricularia, Bipinnaria and Brachiolaria) to the several variants. Later the pluteus form was found to be shared by both echinoids and ophiuroids; and Mortensen (1898) separated the two by the new terms Echinopluteus and Ophiopluteus. Semon, in 1888, proposed one embracing term Dipleurula, for these generally similar bilateral larvae.
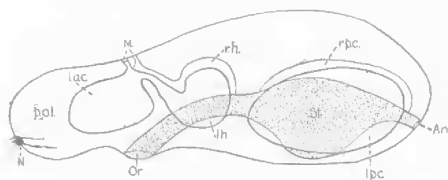

Fig. 7.—The hypothetical Dipleurula (after Bather). *Or.,* mouth; *St.,* stomach; *An.,* anus; *N.,* nerve centre; *p.o.l.,* pre-oral lobe; *M.,* Hydropores; *l.a.c.,* left anterior coelom; *l.h.,* left hydrocoel; *r.h.,* right hydrocoel; *l.p.c.,* left posterior coelom; *r.p.c.,* right posterior coelom.

The Dipleurula, regarded as a consequent ancestral type, has been interpreted by earlier authors (e.g. Bather), and accepted, as a form with the following feature (fig. 7). The body was symmetrical about the sagittal plane and had the ventral side concave. The mouth and anus were present on the ventral side and probably there was an enlargement of the intestine to form a simple stomach. The coelom was divided into paired vessels, the anterior pair being connected to the dorsal surface by a pore or a pair of pores, and continued posteriorly into sacs that were modified to form a paired hydrocoel. The posterior coelomic vessels were separated from the anterior. There was a

pre-oral lobe differentiated as a sense organ, with cilia and a nerve centre from which two gangliated nerves ran symmetrically backwards.

The known larval types (auricularia, bipinnaria, etc.) depart from this generalised form in several ways. Sometimes, for instance, the anterior coelom is not paired, and never is there a perfect pairing of the hydrocoel—the left sac is more developed and sometimes alone is present. In echinoids and ophiuroids the long "arms" of the larvae are supported by a bilaterally arranged skeletal framework.

The perfect symmetry of *Peridionites* suggests that it was closer to the ideal than are the dipleurulan stages of present-day species. It may even be more primitive since, as already noted, it is doubtful whether there was a modification of the medium coelomic sacs to serve as a hydrocoel*.

From the dipleurulan stage the larvae of living species change to the radial adult by a remarkable metamorphosis. On the way, occasionally, it is found that the ciliated bands of the larva are rearranged from a bilateral alignment into five separate rings. This is shown most clearly in the pupa stage of the ontogeny of certain holothurians (see fig. 8); and it seems to
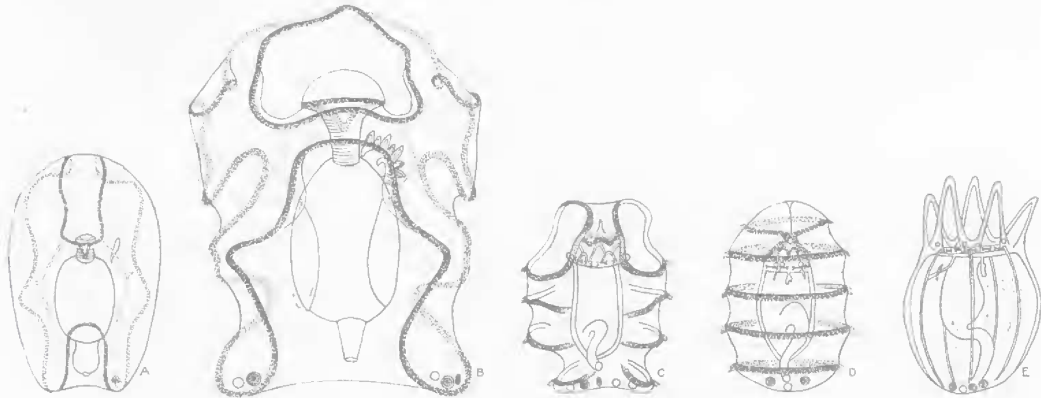

Fig. 8.—Stages in the ontogeny of the holothurian *Synapta digitata* (after Semon). A and B are in the dipleurulan stage; C is transitional to the pupa stage; D is an early form of the pupa stage; and E is the free pentactula stage.

suggest that there are five natural divisions (segments) of the body corresponding to the five ciliated regions. If so the five segments of *Peridionites* become even more significant. It is worthy of note that both the segments of *Peridionites* and the ciliated rings of the larvae are so arranged that two are pre-oral and three post-oral.

In the crinoids the only free larval stage that yet has been found is with *Antedon*. In this the body is bilaterally symmetrical, as with the dipleurula, and the mouth is at a ventral concavity. But five ciliated rings are present,

* It is interesting to recall that MacBride (1918) artificially has reared larvae without a water vascular system.

B

so that probably it is at relatively a higher stage of development than typical dipleurulan larvae. Furthermore incipient stem ossicles occur within it. In the late dipleurulan (brachiolaria) stage of certain asteroids a "sucking disc" develops on the pre-oral lobe by which probably the larva could be attached. Great stress has been placed upon this process by many authorities as being homologous with the fixation of the crinoid larvae (in those forms by a stem). But Bury (1895, p. 93) doubted if there is any homology and Mortensen (1921, p. 239) states that the sucking disc is purely "a secondary adaptation."

In metamorphosis the change is abrupt. The bilaterally symmetrical form is replaced by one that is radial. The body parts rearrange themselves around a new axis. In those forms (echinoids and ophiuroids) in which previously there was a bilateral skeleton this skeleton is not merely modified.
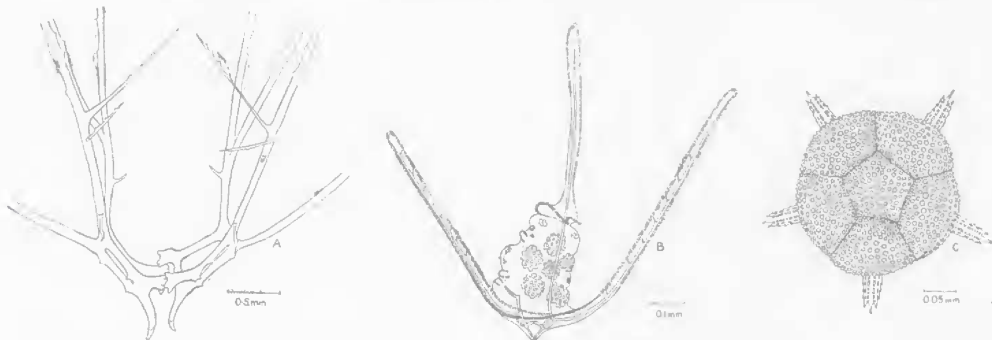

Fig. 9.—Skeletal forms in ophiuroid larvae. A, the bilateral skeleton of an ophiopluteus (dipleurula stage). B, a phase during metamorphosis with the bilateral skeleton not wholly resorbed and the radial skeleton beginning to form. C, the skeleton of a form in the pentactula stage. (A and B after Mortensen; C after Chadwick.)

It is resorbed and a new skeleton conforming to the radial plan appears in its place (fig. 9). To this first radial stage Semon (1888) gave the name Pentactula. In the comatulid crinoids it is fixed. In all other recent forms that have been investigated it is free.

The holothuroids of course have no continuous skeleton, but in all other groups of the Eleutherozoa the skeleton in the pentactula stage is similar. It consists of eleven plates (fig. 9c)—a dorso-centrale, five radials and five terminals. There are certain class differences in the appearance of these plates that Sladen (1884) thought might have a phylogenetic significance. In the echinoids, except for the dorso-centrale which is replaced by the periproct, the initial plates are emphasised to form the genital and ocular plates and constitute the apical disc in the corona of the fully developed adult. In certain early asteroids, notably the genus *Hudsonaster* (see Schuchert, 1915), the eleven initial plates are retained as an almost equally accentuated apical system; but generally in the asteroids and the ophiuroids, as the skeleton grows by the addition of the many other plates, the initial eleven cease to be a recognisable, circumscribed group.

From these agreements an adult form with a skeleton corresponding with that of the larval free pentactula should occur in early strata. *Cymbionites* virtually is this. It has a cycle of five radial plates, there is a spasmodically appearing dorso-centrale, and all plates are united into a simple, free, capsule-like theca. A cycle of five terminals does not develop; but the spherulitic growth of the skeleton is such that it is likely that other and closely similar genera have arisen in which the full complement of eleven plates occurs. The Cycloidea, represented at present solely by *Cymbionites,* have a claim to represent the ancestral, free pentactula comparable with that of the Cyamoidea to be the early dipleurula; and since in ontogeny the free pentactula is the starting point in the development of asteroids, ophiuroids and echinoids, so in phylogeny the Cycloidea may be regarded, I would suggest, as the immediate common ancestor of these three classes.

In ontogeny, as already noted, the change from dipleurula to pentactula is abrupt, the skeleton elements of the two having nothing in common. The difference between the skeletons of *Peridionites* and *Cymbionites* is comparably great. In the former there is no fibrous form and the skeleton is moulded to the bilateral body. In the latter fibrous elements develop, spherulitic growth is initiated, takes control and produces a radial, pentameral skeleton to which the body is adapted, modified by necessity with considerable rearrangement of parts. If Cyamoidea and Cycloidea correctly are interpreted as representing the dipleurula and pentactula stages, then in this there is a simple explanation of the abrupt metamorphosis in echinoderm ontogeny. All that was needed was a change from non-fibrous to fibrous calcite as the skeletal element—or, in other words, a more formal arrangement of the cells in the mesenchyme so that regular, fibrous secretion was possible.

The pentactula larva of crinoids, as represented by *Antedon,* is fixed firmly by a stalk. Such an attached pentactula was called Pentactaea by Semon (1888) who claimed that an early form of this type would be the ancestor of all modern echinoderms, a claim that these new discoveries to a large extent refute. But the stem in *Antedon* starts to develop in the previous larval stage—the pelagic, bilateral larva with ciliated rings. The attachment of the crinoids thus appears to date from a stage at the close of its dipleurulan history; and pentameral, radial growth may be considered to have developed parallel to the Cycloidea and, presumably, in an analogous spherulitic mode.

ASPECTS OF PHYLOGENY.

The long-desired reconciliation between the ontogeny and palaeontology of the echinoderms was not possible so long as all the earliest and supposedly the most primitive genera were attached. An unattached, radially symmetrical body of simple plating, such as occurs in early growth stages, was not known. The majority of those who wrote were satisfied that, whereas some unknown, unattached, bilaterally symmetrical echinoderm (the Dipleurula) must have

existed, an unattached radial form was not necessary. Free radial types, so
ran the argument, must come after the fixed ("radial symmetry being, it would
appear, a consequence of fixation"—Bather, 1900, p. 9). Semon (1888), so far
as I can discover, seems first to have enunciated this idea which, developed by
other specialists, has come to be regarded almost as a law of echinodermal
development. Accordingly fixed forms like those of the early Palaeozoic were
taken to be the primitive types from which the unattached echinoderms have
evolved. The presence of free, radial, larval stages was dismissed with such
specious arguments as: "changes that, in phylogeny, must have succeeded
fixation now precede it" (Bather, 1900, p. 9); or else it was implied that a
fixed stage had been suppressed in the ontogeny of echinoids, ophiuroids and
holothuroids by a process of accelerated development. Considerable reliance,
accordingly, was placed upon the temporarily attached stage through which
some asteroids go. This was a weak point in argument; for, as already noted,
some experienced specialists believe that this transient attachment is in no wise
homologous with the fixation of the crinoids.

It is somewhat surprising to realise that a fixed ancestry was considered
essential for any radial symmetry. The most perfect of all radial animals and
plants, the Radiolaria and the Diatoms, pass through no fixed stage. Among
the Coelenterata it is only the pelagic types, the medusae, that attain the perfect
radial form.

At its best the reasoning was illogical. Bury (1895), it should be
remembered, sounded a note of caution but was hardly heard. In an incisive
essay he justly affirmed that if all present-day echinoderms were derived from
fixed forms then ontogeny is misleading; and the obligation still was with
palaeontologists (as indeed it has been ever since) to establish a fixed ancestry.

However the needs for this tortuous type of phylogeny are removed when
two free, fossil forms are known, almost as early as echinoderms have been
recorded, agreeing morphologically with the dipleurula and free pentactula
stages. Not only individually are they pertinently comparable with ontogenetic
stages; but the simple, spherulitic growth of the radial form (*Cymbionites*)
indicates that the attainment of radial, pentameral symmetry was independent
of fixed conditions.

One other argument, hitherto unassailable but, in the light of this new
evidence, of questionable validity, must be noted. It was, perhaps, most clearly
expressed by Bather (1900, p. 8) in the words: "By a remarkable metamorphosis,
varying in its detail but presenting some common features in the different
classes, the almost bilaterally symmetric larva is transformed into the almost
radially symmetric adult. This metamorphosis undoubtedly represents the
changes that occurred in the early history of the classes; and the extraordinary
difficulties of interpretation are due to the enormous compression of that
history, the elimination in some cases of unnecessary stages, and the unequal

acceleration of others.'' This metamorphosis is one of the most striking and abrupt changes in the ontogeny of invertebrates, and hitherto it has not received a satisfactory explanation. But the changes, already assessed, that took place by the development of spherulitic growth were themselves abrupt so that there may be now no need to postulate an ''enormous compression'' or an ''elimination of unnecessary stages'' in phylogeny.

Thus, if these two forms are correctly interpreted, the palaeontological evidence and the succession in ontogeny no longer are at variance. Early fossil forms corresponding to the essential larval stages are known and an explanation of the abrupt change in metamorphosis is available; so that the ontogeny of a species may be claimed as a true epitome of the phylogeny of its group. Based upon what is known of larval stages and is summarised in the preceding chapter the consequences of this would be expressed as follows.

Asteroidea, Ophiuroidea and Echinoidea are derived from Cycloidea and they, in previous sequence, came from Cyamoidea. The Crinoidea arose from Cyamoidea at about the stage when it was evolving into the cycloids. About Holothuroidea, that have no interlocking skeleton, no comments are possible from the evidence of these fossils. In 1911, it should be noted, Walcott described as holothuroids a number of new genera and species from the Middle Cambrian of British Columbia. Some comment arose about the correctness of the biological grouping of these forms. A. H. Clark (1912) accepted the forms as holothurians and published an interesting restoration of one of them, *Eldonia ludwigi*. However in the same year H. L. Clark (1912) refused to accept them as echinoderms. More recently Croneis and McCormack (1932), though non-committal in their writings (p. 127) about the echinodermal nature of these forms, nevertheless implied in their evolutionary diagram (p. 135) that they were holothurians. I do not propose to enter into this controversy other than to remark that *Eldonia*, as restored by A. H. Clark, is a form that would fit neatly the calyx of such an echinoderm as *Cymbionites*, so that some relationship might be considered; although just as easily, from that restoration, it could be claimed as a coelenterate. It may be pertinent, also, to recall a suggestion made by Bell (1891) that since the holothurians are non-calicular and do not have gonads arranged pentamerally they may have departed rather early from the common stock. The other great groups of echinoderms are all extinct and of them we have no ontogenetic knowledge; but from other evidence they, too, may be brought into conspectus.

The Cystida, Blastoidea, Edrioasteroidea and Crinoidea are related by the common bonds of firm attachment and radial symmetry. Even in such irregularly plated genera as *Aristocystis* and *Sinocystis* the first (aboral) plates are a regular cycle suggesting that, whatever be their subsequent history, these forms began as radial types. It would be idle to enter into a discussion of the interrelations of these classes. As a related group they may be regarded, from the evidence of the crinoids, their one surviving member, as having arisen from the developing echinodermal stock in the closing phase of the dipleurulan period.

If the class Machaeridia, established by Withers (1926), be correctly placed in the echinoderms, as the evidence seems satisfactorily to suggest, its closest affinities are with the Carpoidea (Jaekel, 1900), as Bather (1926 and 1929) has noted. Each group is bilaterally and not radially symmetrical, and with each there has been some speculation whether, accordingly, it could represent the long-sought Dipleurula*. Neither, of course, truly is a dipleurulan type, for each is multi-plated beyond what is expected of such a form. But they may be related to Cyamoidea, interpreting that as the dipleurulan group. The Machaeridia, being longitudinally plated by a succession of similar structures, are suggestively more segmented than *Peridionites*; so that conceivably they arose either from very primitive cyamoids or they are a collateral branch from an even less specialised, segmented form with echinodermal characters only incipient—either that or their greater segmentation is secondarily derived.

It is customary to place the Carpoidea in the Pelmatozoa, and thereto Bather (1929) has allotted the recently established Machaeridia. But not only have these two groups no sign of the radial arrangement that, in some degree, is found in ordinary pelmatozoans, but if they were attached at all their attachment was different. Withers has noted that the proximal plates in the skeleton or test of Machaeridia are slightly modified, and a hint was given that thereby they might have been attached. But the figures do not suggest attachment and all specimens that were described were isolated. The carpoids have a long "stem" that often is similar to the whole skeleton of a machaeridian, but it tapers and, so far as I am aware, no such structure has been figured showing one of these forms anchored to a foreign body. Maybe in many forms it was only a tail-like feature.

In such manner these two groups differ from all other echinoderms and were better kept distinct. Tentatively I suggest that they represent a separate group (a sub-phylum it would have to be) for which the term HOMALOZOA (ὁμαλός flat, ζῷον living creature) would be appropriate.

Graphically these ideas are embodied in the accompanying diagram.

There still is, in the vertical range of the unattached echinoderms, a hiatus that makes perfect palaeontological accord impossible. But this is readily to be understood when one considers the great rarity of early Palaeozoic Eleutherozoa, the fact that for all these years Cyamoidea and Cycloidea have remained undiscovered, and that it was only a few years ago that Ordovician echinoids

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* *See* Walther (1886) and Haeckel (1896) for the Carpoidea and Bather (1926 and 1929) for the Machaeridia. In passing it may be noted that Fritsch (1909, p. 797) suggested that an Ordovician fossil from Bohemia, the *Furca bohemica* of Barrande, was the larval stage of a crinoid; but Jaekel (*fide* Mortensen, 1921, p. 233) places that form as an arthropod and not an echinoderm.

were discovered in relatively well-searched Britain.*   One may venture to suppose that other and later cycloids eventually will be found, and maybe earlier eleutherozoans, to reduce this gap in sequence.   The great wealth of echinodermal limestones in the Cambrian of Queensland itself offers some hope of this.

Two other aspects remain that require only brief mention—the origin of the cyamoids and the relationship to primitive Chordata.   The perfect segmentation of *Peridionites* (and incidentally the even more numerous segments of Machaeridia) suggests that its ancestors were well-segmented, coelomate creatures.   What they were it is not possible to say.   The annelids fulfil such requirements, but there are difficulties about an annelid ancestry (particularly in essential differences in segmentation of the ovum in Annelida and Echinodermata).

Unknown, Segmented
Coelomate Ancestor
Homalozoa
Cyamoidea
Pelmatozoa
Cycloidea
Eleutherozoa
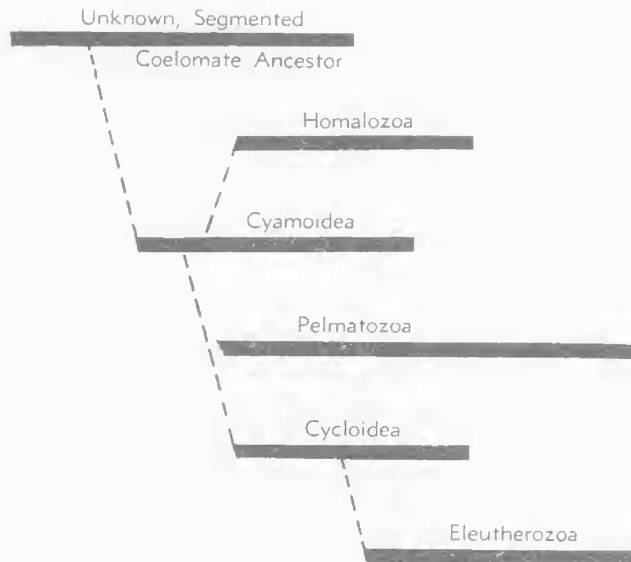
The primitive chordate *Balanoglossus* and its relatives have a larval form (Tornaria) named by Müller and of the same type as the Dipleurula.   Many authors have thought that thereby there might be some common ancestor to both the early chordates and the echinoderms.   The discovery of *Peridionites* does not bring these two groups very much closer; for *Peridionites* still is a typical echinoderm in its skeletal structures and so is not a member of a common ancestral group.

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* *Myriastiches gigas*, an English echinoid, was recorded as long ago as 1899 by Sollas from a single specimen; but it does not seem to have been recognised as Ordovician until 1934, when Bather and Spencer described a second Ordovician species from Great Britain— *Aulechinus grayae* from Girvan (Scotland).

CONCLUSIONS.

1. Two early Middle Cambrian echinoderms are described, each of them unattached and having a skeleton composed of very few plates with typical, unit calcite cleavage.

2. One (*Peridionites*), of the new class Cyamoidea, is bilaterally symmetrical, having a calyx of five precisely arranged plates without a fibrous structure. There is ample evidence that the body was arranged in five segments with perfectly paired structures.

3. In the arrangements of its parts *Peridionites* corresponds remarkably well with the hypothetical Dipleurula, though in some features it may be even more primitive than was expected of the Dipleurula. A reconstruction of the body parts is possible and is shown in text figure 3.

4. The other (*Cymbionites*), of the new class Cycloidea, is radially symmetrical, with a theca composed of five very variably arranged plates with sometimes small accessory plates (centrale and radials).

5. *Cymbionites* corresponds with the free pentactula stage in the ontogeny of the Eleutherozoa, although the five terminal plates do not occur.

6. The skeleton of *Cymbionites* is formed of radial fibres arranged according to the mode and variations of spherulitic growth. The formation of the plates clearly is subsidiary to the spherulitic pattern; and so it is suggested that the form of the skeleton and the pentamerism of its parts were determined by the almost inorganic control of typical, spherulitic increase, and that the body adapted itself to this new mode.

7. By this change, through spherulitic growth, an explanation is offered of the metamorphosis in echinoderm ontogeny—being due to the cells of the mesoderm developing in such fashion that multi-spicular secretion was possible.

8. It is believed that the relatively great mass of the skeleton in these forms favoured the spherulitic mode when fibrous secretion began. Also since pentamerism was a consequence of this mode of growth, and since *Peridionites* already had five definite segments, a torsion to adapt the two independent pentameral developments (body and skeleton) may be the explanation of the torsion of body parts during metamorphosis in ontogeny. Thus to the unusual coincidence of these factors (massive skeleton and independent pentamerism of body and skeleton), it is suggested, are due the unique features of the metamorphosis of the echinoderms.

9. An attached stage in the phylogeny of the Eleutherozoa generally has been postulated although without confirmation in ontogeny. The existence of these two early forms and their correspondence, morphologically, with the two chief larval stages, makes it unnecessary to require an attached stage in the ancestry of the Eleutherozoa.

10. From comparative studies it is suggested that the Homalozoa (that is, Machaeridia and Carpoidea) were derived from early Cyamoidea or from an even more primitive group; and that Pelmatozoa (Cystida, Blastoidea, Edrioasteroidea and Crinoidea) arose from Cyamoidea at about the stage of transition to Cycloidea.

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EXPLANATION OF PLATES.

PLATE I.
(All figures natural size.)

Fig. 1. *Cymbionites craticula* sp. nov. Limestone showing the concentration of individuals. Complete specimens are seen in ventral, lateral and dorsal views. A natural transverse section, through the lower part of the calyx, is shown in the centre of the photograph, with five plates of approximately equal size.

Fig. 2. *Peridionites navicula* sp. nov. Limestone showing isolated plates of the species, most of them end plates. Two plates of *Eocystis* (?) *sp.* also are to be seen.

Fig. 3. *Cymbionites craticula* sp. nov. A specimen showing isolated plates, each of them typically wedge-shaped.

PLATE II.
(All figures natural size unless otherwise stated.)

Figs. 1–9. *Peridionites navicula* sp. nov. 1a, b, lateral and ventral views of a typical complete specimen. 2, 3 and 4, lateral views of three specimens of a rather taller type. 5, ventral view of a more obese form. 6, a typical specimen with the apical plate missing. 7a, b, a specimen similar to fig. 6 with the sutures of the medio-lateral plate etched; 7b is an enlargement (× 2) of this specimen, the *holotype*. 8a, b, ventral view of another specimen (8b is enlarged two diameters). 9a, b, microphotographs through a complete specimen. 9a (magnified 9 diameters) illustrates the general form. The black dots indicate the outline of the Central Cleft. The irregularly porous nature of the skeleton may be seen, the pores aligned generally in a radial fashion. Figure 9b is a greater magnification (enlarged 30 diameters) of that portion of 9a within the four white dots. The irregular pores of the skeleton may be noticed.

Figs. 10–24. *Cymbionites craticula* sp. nov. 10, an almost vertical microsection (enlarged 13 diameters) through the calyx. The following features should be noticed (see also text-fig. 5):

   i. The unity of the fibrous development throughout the skeleton.

   ii. The grouping of the plates according to the tufts.

   iii. The crowding out of a small plate near the base of the calyx by the growth of neighbouring tufts.

   iv. The discordance between the two uppermost sutures and the fibres—that on the left discordant only towards the outer edge, that on the right continuously discordant.

   v. The cessation of the upper, right suture in outwards development.

   vi. The well developed growth lines.

Fig. 11 is a naturally etched specimen, the silicified margins of the outer and inner walls, as well as the five sutures, stand out in natural relief.

Figs 12–22 (a and b) show ventral and lateral views of eleven specimens, illustrating the variation in shape. Fig. 12 is the *holotype*.

Fig. 23 is a ventral view (× 2) of a form with seven radial plates and a centrale.

Fig. 24 (× 2) is a ventral view of a slightly etched specimen showing that the sutures correspond sometimes with the crests and sometimes with the dips in the scalloped margin of the calyx.

PLATE III.

Cymbionites craticula sp. nov.

Four microphotographs of transverse sections through plates of the theca.

Fig. 1. Section of one plate near the calical wall (the bounding sutures are at the top and bottom left corners). The fibres occur as a simple tuft contained within the limits of the plate. ($\times$ 25 diameters.)

Fig. 2. A specimen in similar aspect to fig. 1, but with the fibres arranged in a double tuft. ($\times$ 50 diameters.)

Fig. 3. A section dorsal to the calyx showing fibres arranged in one plume that forms the whole theca. Sutures are not developed. ($\times$ 25 diameters.)

Fig. 4. A section dorsal to the calyx and midway to the outer edge, showing a suture discordant with the fibres. Although the fibres are continuous across the suture they have differing optical properties on either side. ($\times$ 50 diameters.)

PLATE IV.

Cymbionites craticula sp. nov.

Four microphotographs of transverse sections through plates of the theca.

Fig. 1. A specimen with plumose growth, showing a small plate starting to develop with very strong sutures bounding a small plume, but the sutures soon cease and the plate does not separate. ($\times$ 25 diameters.)

Fig. 2. A section across the specimen illustrated in text fig. 7D, showing two plumes separated by a suture. The radial, plumose growth is very well illustrated, and also the typical symmetry of fibres across a suture. ($\times$ 50 diameters.)

Fig. 3. The centre portion of the plume of fig. 2 enlarged 230 diameters, showing the fibres and the interstitial meshwork.

Fig. 4. Another portion of the same slide enlarged 750 diameters, in which there are transverse and longitudinal sections of the fibres, and in which the relations to the interstitial meshwork can be seen.

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The specimens illustrated in text-figures and on plates bear the following numbers in the catalogue of the Department of Geology, the University of Queensland:

Peridionites navicula:

Plate I, fig. 2 (5398).

Plate II, fig. 1 (5399), fig. 2 (5400), fig. 3 (5401), fig. 4 (5402), fig. 5 (5403). fig. 6 (5405), fig. 7 (5404—holotype), fig. 8 (5406), fig. 9 (5407).

Cymbionites craticula:

Plate I, fig. 1 (5408), fig. 3 (5421).

Plate II, fig. 10 (5422), fig. 11 (5423), fig. 12 (5409—holotype), fig. 13 (5410), fig. 14 (5411), fig. 15 (5412), fig. 16 (5413), fig. 17 (5414), fig. 18 (5415), fig. 19 (5416), fig. 20 (5417), fig. 21 (5418), fig. 22 (5419), fig. 23 (5435), fig. 24 (5420).

Plate III, fig. 1 (5424), fig. 2 (5425), fig. 3 (5426), fig. 4 (5427).

Plate IV, fig. 1 (5428), figs. 2, 3 and 4 (5429).

Text-fig. 6A (5430), 6B (5424), 6C (5431), 6D (5429), 6E (5433), 6F (5434), 6G (5435).